Loss of attentional stimulus selection after extrastriate cortical lesions in macaques

Peter De Weerd[1,3], Modesto R. Peralta III[1], Robert Desimone[2] and Leslie G. Ungerleider[1]

[1] Laboratory of Brain and Cognition, NIMH, 10 Center Drive, Bethesda, Maryland 20892, USA

[2] Laboratory of Neuropsychology, NIMH, 49 Convent Drive, Bethesda, Maryland 20892, USA

[3] Current address: University of Arizona, College of Social and Behavioral Sciences, Department of Psychology, P.O. Box 210068, Tucson, Arizona 85721-0068, USA

Correspondence should be addressed to P.D. (pdeweerd@u.arizona.edu)

Many objects in natural visual scenes compete for attention. To identify the neural mechanisms necessary for visual attention, we made restricted lesions, affecting different quadrants of the visual field but leaving one quadrant intact, in extrastriate cortical areas V4 and TEO of two monkeys. Monkeys were trained to discriminate the orientation of a target grating surrounded by distracters. As distracter contrast increased, performance deteriorated in quadrants affected by V4 and TEO lesions, but not in the normal quadrant. Performance in affected quadrants was restored by increasing the contrast of the target relative to distracters. Thus, without V4 and TEO, visual attention is 'captured' by strong stimuli, regardless of their behavioral relevance.

Cortical areas V4 and TEO are two higher-order components of the ventral processing stream of the visual system, important for object recognition in primates[1]. Selectivity of neurons in V4 (refs. 2–6) and inferior temporal cortex[7–13] including area TEO for object features such as color, texture and shape supports an important role for these two areas in object recognition. However, V4 or TEO lesions reveal only limited deficits in object feature discrimination. Color perception deficits following V4 lesions, for example, are mild[14,15]. Likewise, although deficits are reported for various types of texture, pattern, and shape discriminations after lesions in V4 (refs. 16–20), TEO[21], V4+TEO combined[22] and the inferior temporal cortex including TEO and TE[23–26], many discriminations remain possible following these lesions, albeit with diminished performance.

Contributions of ventral stream areas to object perception are typically examined using isolated stimuli on a blank background. In more realistic environments, the visual system must recognize objects in the presence of a multitude of other objects. We hypothesized that testing object perception under such conditions following cortical lesions might uncover contributions of ventral stream areas to visual perception.

Human studies show that, when multiple objects are displayed together, subjects cannot process and recognize all objects simultaneously[27–30]. Rather, only one or, at most, a few behaviorally relevant objects (targets) are processed at the cost of irrelevant objects (distracters). In line with these behavioral findings, neuronal recordings in monkey ventral stream areas reveal that behavioral relevance strongly influences neuronal responses to simultaneously presented stimuli. When two stimuli are placed inside a cell's receptive field (RF) in areas V2, V4, TEO or TE, responses are determined primarily by the behaviorally relevant, or attended stimulus[31–38]. Thus, the influence of ignored stimuli upon neuronal responses is strongly reduced. By contrast, when attention is directed away from the RF, responses to a pair of stimuli within the RF are typically dominated by whichever stimulus has the higher contrast (J.H. Reynolds *et al.*, *Soc. Neurosci. Abstr.* **22**, 1197, 1996; J.H. Reynolds & R.D., *Soc. Neurosci. Abstr.* **23**, 302, 1997). These findings support a 'biased competition' account of attention, in which multiple objects within a cell's RF compete for control over the cell's response and attentional inputs favor relevant objects[36,39]. In this view, 'top-down' attentional influences can overrule 'bottom-up' stimulus-driven competition among stimuli in ventral stream areas. We predicted, therefore, that removal of one or more of those areas in monkeys (**Fig. 1a**) should specifically impair selective processing of a relevant stimulus in the presence of competing distracters.

Physiological effects of attention have been described in all extrastriate areas of the ventral stream[31–36]. Because of multiple anatomical interconnections, a lesion in one ventral stream area might easily be compensated for by another one, limiting behavioral deficits. Indeed, in addition to the major anatomical pathways connecting V1 to V2, V2 to V4, V4 to TEO and TEO to TE[1,40], direct pathways also exist from V2 to TEO, bypassing V4, from V1 to V4, bypassing V2, and from V4 to TE, bypassing TEO[41,42]. Thus, removal of a single area will likely reveal only a limited deficit, as the loss may be largely compensated for by such bypass pathways. We therefore compared deficits caused by lesions in V4 or TEO alone with those caused by a combined lesions of V4 and TEO. Retinotopic representation of the visual field in areas V4 (ref. 43) and TEO[44] allowed us to place the V4 lesion to affect one visual field quadrant and the TEO lesion to affect another, with both affecting a third quadrant. The remaining intact quadrant served as a normal control. While the monkeys maintained fixation on a central spot, they discriminated stimuli presented away from fixation in each quadrant, permitting comparison of performance in three different lesion conditions with normal performance (**Fig. 1b**; Methods).

Results

Effects of distracters on orientation discrimination

In Experiment 1, two monkeys were trained to discriminate grating orientation and their orientation thresholds (smallest detectable differences) were measured (**Fig. 1c**, Methods). Distracters were then added to the display and their contrasts were manipulated by reducing or increasing luminance relative to the background (**Fig. 2a**). In the three lesion-affected quadrants, orientation thresholds for target gratings (50% contrast) were larger with surrounding distracters than without. In the normal quadrant, orientation judgments were unaffected by distracters (**Fig. 2b**). Greater distracter-induced threshold increases were observed in the visual field quadrant affected by lesions in both V4 and TEO (V4+TEO quadrant) than in quadrants affected by a lesion in V4 or TEO alone. In all three lesion quadrants, increases in distracter contrast reduced target-grating effectiveness in guiding behavior.

Without distracters, thresholds in the lesion quadrants were higher than those in the normal quadrant (0% distracter contrast, **Fig. 2b**), indicating sensory deficits in orientation discrimination. Therefore, thresholds measured with distracters in the lesion quadrants reflect combined distracter-induced and distracter-independent sensory deficits. To isolate distracter-induced (attention) deficits from sensory deficits, baseline thresholds measured without distracters were subtracted from thresholds measured with distracters in each quadrant for the remainder of the experiments.

Effect of relative contrast between target and distracters

If impairments caused by distracters in the lesion-affected quadrants reflected competition between stimuli no longer biased by attention (or biased to a lesser extent), then impairments should be observed for any combination in which grating contrast is much lower than distracter contrast. Likewise, performance should be restored by increasing grating contrast above that of the distracters. In addition, the competition idea predicts that, without distracters, impairments remain stable in lesion-affected quadrants when grating contrast is decreased. In experiment 2, we tested these predictions by varying both grating and distracter contrast in each quadrant (**Fig. 3a**).

Thresholds in the V4+TEO quadrant increased ~40° above baseline when distracters of 50% contrast were placed around a grating of similar contrast (triangles, **Fig. 3b**; pooled over monkeys), in agreement with the previous experiment. Reducing grating contrast below that of the distracters further impaired performance, ultimately raising threshold beyond a measurable range. Thus, the animals were severely impaired in discriminating a grating surrounded by distracters of equal or higher contrast. Conversely, grating orientation thresholds were only slightly elevated by placing distracters of 10% contrast around the grating (squares, **Fig. 3b**; V4+TEO quadrant) or by increasing grating contrast well above that of the distracters relative to thresholds obtained with the grating presented alone (circles, **Fig. 3b**; V4+TEO quadrant). Thus, the animals were able to see, 'attend to' and discriminate the grating if its contrast was much higher than that of the distracters. Taken together, the results suggest that the higher contrast stimulus, whether target or distracter, dominated activity in intact visual areas outside the lesion. Thus, the capacity for selective attention to one stimulus over another was lost. We found similar but less pronounced effects of the distracters in the two quadrants affected only by one lesion in V4 or in TEO (**Fig. 3b**), suggesting one of these two areas can partially compensate for a lesion in the other.

In contrast, in the normal quadrant, monkeys could easily discriminate the grating's orientation at all contrast levels despite strong distracters (**Fig. 3b**). Indeed, although reducing grating contrast

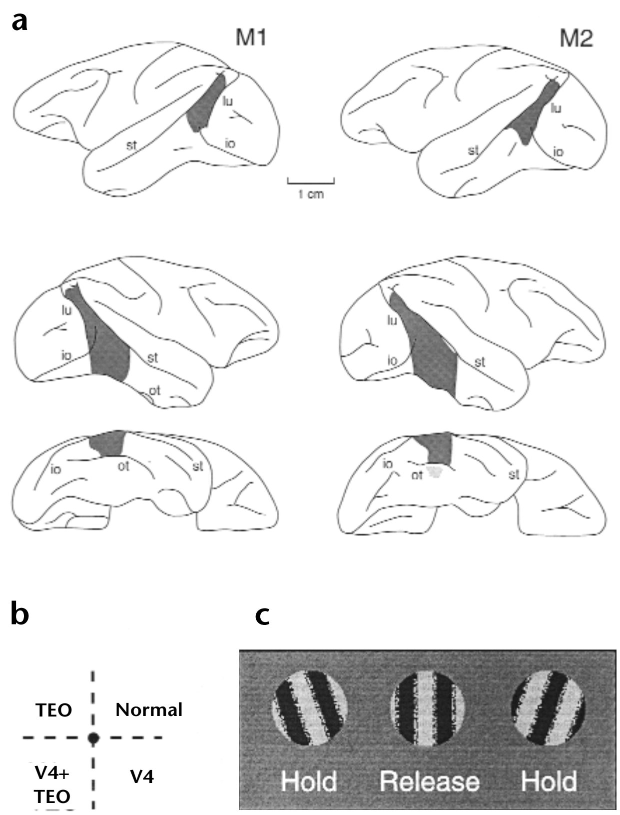
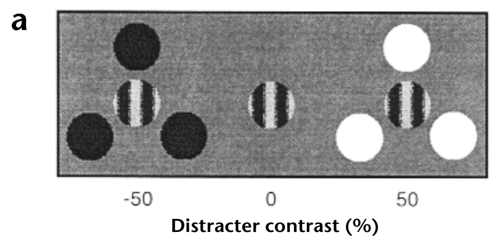


Fig. 1. Extent of V4 and TEO lesions in monkeys M1 and M2. **(a)** Lateral view of the left hemisphere showing a lesion (dark shading) in the dorsal part of V4 for monkeys M1 and M2, shown on top. Below are lateral and ventral views of the right hemisphere showing a lesion in the dorsal part of V4 and in TEO in M1 and M2. MRI scans suggest unintended damage medial to 'ot' in monkey M2 (lighter shading). Abbrevations: lu, lunate sulcus; st, superior temporal sulcus; io, inferior occipital sulcus; ot, occipital temporal sulcus. **(b)** Distribution of lesion effects in the four quadrants of the visual field, derived from retinotopy in areas V4 and TEO (see Methods). **(c)** Grating stimuli and discrimination task. Monkeys fixated a dot in the middle of the monitor (**Fig. 1b**), and grabbed a bar to initiate a discrimination trial. Gratings were presented away from fixation (see Methods for details). Monkeys received juice for releasing the bar during or within 600 ms after a 600-ms presentation of a vertical grating. Monkeys were rewarded for holding the bar for 1200 ms on presentation of nonvertical gratings.

modestly but significantly increased orientation thresholds in the normal quadrant ($F_{6,131} = 6.278$, $p < 0.001$), there was no effect of the distracters at any contrast ($F_{2,131} = 0.88$, $p = 0.417$). Even surrounding a barely visible grating (2.5% contrast) by bright distracters (50% contrast) did not significantly affect thresholds ($F_{1,131} = 0.106$, $p = 0.745$), demonstrating that attention efficiently enhances a physically weak stimulus over physically strong distracters. Furthermore, decreasing grating contrast in the absence of distracters similarly increased thresholds in the lesion quadrants and in the normal quadrant ($F_{18,196} = 1.256$, $p = 0.221$), although discrimination of a low-contrast grating presumably demanded attention. Thus, lesions did not generally impair attentional capacity but, rather, specifically impaired biasing of competition between multiple objects by attention. These distracter-induced deficits were reproduced in both monkeys over several postoperative years, indicating that the deficits were permanent.



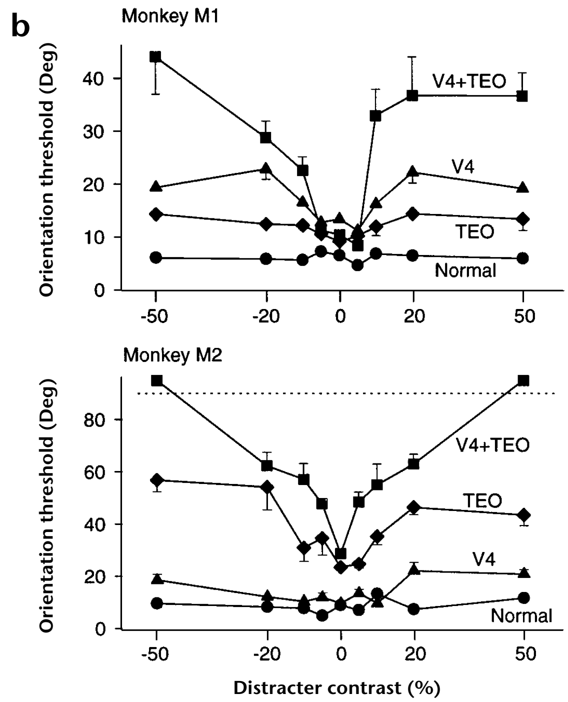


Fig. 2. Effects of grating and distracter contrast on grating orientation discrimination. Distracter contrast is the contrast between distracter and background luminance; grating contrast is the contrast between dark and light stripes (Michelson indices, see Methods). Other stimulus parameters were as in experiment 1 (Methods). **(a)** Experimental design with 9 distracter conditions; dark distracters (–50% contrast), white distracters (50% contrast) and without distracters (0% contrast) are shown. Grating contrast was 50%. Typical V4 and TEO cells[43,44] contain the target and much of the distracters in their RF. Distracter positions were varied, but the grating position was constant. **(b)** Thresholds as a function of distracter contrast for each monkey in each visual field quadrant. Data points are averages typically based on four thresholds; error bars indicate s.e.; absence of an error bar indicates a s.e. smaller than the symbol size. Symbols above upper dotted line indicate conditions in which no threshold could be determined in at least half of the measurements (monkey M2).

Effect of the distance between target and distracters

In recording studies, attention effects are stronger when two competing stimuli are located within the same RF than when spatially separated[33,34,36]. To test the role of stimulus spacing, in experiment 3 we determined orientation thresholds for gratings with distracters placed inside the same quadrant (inside condition, **Fig. 4a**)or with distracters placed outside (outside condition). For each quadrant, we measured distracter-induced increases in threshold (**Fig. 4b**, pooled results). No significant effects of distracters were found in the normal quadrant ($F_{1,171} = 2.720$, $p = 0.101$). In the three lesion-affected quadrants combined, threshold increases caused by inside distracters ($F_{1,171} = 47.980$, $p < 0.001$) but not by outside distracters ($F_{1,171} = 1.726$, $p = 0.191$) were significant. Lack of effect of outside distracters may be because RFs in V4 and TEO are within the same quadrant and are therefore unlikely to mediate competition between objects separated over a larger range. More anterior portions of inferior temporal cortex, where RFs often extend into all quadrants, are more likely to mediate competition between stimuli spaced as widely as in the outside condition[31].

In monkey M2, we investigated the relation of deficits caused by distracters in lesioned quadrants to RF size in V4 and TEO. We reduced stimulus diameters and measured distracter-induced threshold increases above baseline using stimulus arrays with different spacings between elements and overall sizes (**Fig. 4c**). The small gratings (see Methods) gave larger baseline thresholds (**Fig. 4c**, legend) and distracter-induced threshold increases above baseline than in previous experiments. For a 5.6° × 5.6° array, threshold increases were similar in the V4 and in the TEO quadrants (**Fig. 4d**), presumably because the array was small enough to be contained within typical V4 and TEO RFs (dotted lines, **Fig. 4c**). Increasing the array size from 5.6° to 7.4° and 9.2° strongly reduced the effect of distracters in the V4 quadrant ($F_{1,164} = 23.908$, $p < 0.001$)], but not in the TEO quadrant ($F_{1,171} = 0.011$, $p = 0.918$). The distracter effect was significantly reduced in the TEO quadrant only if distracters were outside the quadrant ($F_{1,164} = 25.597$, $p < 0.001$). In the normal quadrant, distracters had no effect ($F_{1,164} = 0.000$, $p = 0.989$). Thus, distracter-induced deficits caused by V4 and TEO lesions were maximal for stimulus arrays roughly the size of their typical RFs and decreased for larger arrays (arrows, **Fig. 4d**), suggesting that neuronal RF size limits the spatial extent over which that visual area can bias competition between stimuli.

Grating detection and acuity

In contrast to the severe effect of the lesions on ability to discriminate grating orientation in the presence of distracters, we found no deficit in the monkeys' ability to detect a vertical grating among distracters in experiment 4; that is, perform a simple 'pop-out' task. On half of the trials, the standard array was presented with a vertical grating in the middle and three distracters; on the other half, four luminance distracters were presented. All stimuli were at 50% contrast. Monkeys were rewarded for releasing a bar when the array contained the grating; both performed at 97% correct or better in this task in normal and lesion-affected quadrants. The absence of detection task deficits contrasts with the strong impairment by distracters of target feature discrimination in lesion-affected quadrants. Deficits were observed when the monkeys were required to discriminate stimulus features in the presence of competing distracters, but not when simply required to detect a stimulus differing from other background objects, suggesting that the monkeys could detect the target but could not make out its features. Furthermore, the distracter-induced deficits found in this study cannot be due to impaired acuity. The spatial frequency of the grating ranged from 0.6 to 2 cycles per degree (cpd) in the different experiments (see Methods), but monkey M1 showed no deficit in discriminating gratings of up to 16 cpd from homogeneous gray stimuli of matched luminance, size and eccentricity ($F_{3,48} = 0.472$, $p = 0.703$) in lesion-affected quadrants. Monkey M2 showed a small deficit at 16 cpd in all lesion-affected quadrants ($F_{1,121} = 29.713$, $p < 0.001$), but not at spatial frequencies of 8 cpd or lower ($F_{3,95} = 2.071$, $p = 0.109$).

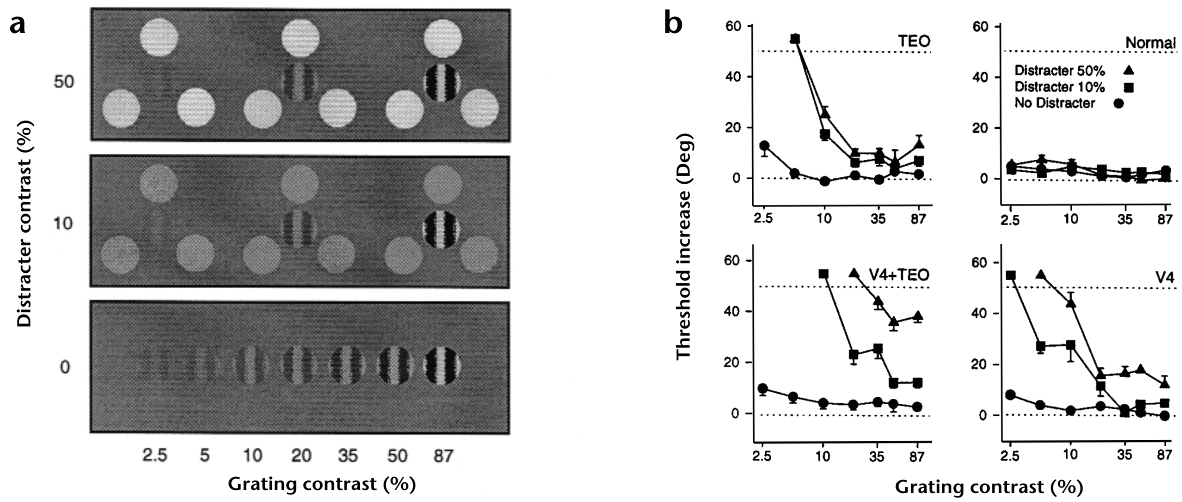


Fig. 3. Effects of grating and distracter contrast on grating orientation discrimination. **(a)** Experimental design with three distracter conditions (no distracters, 10% and 50% distracter contrast) and seven grating contrasts. Other stimulus parameters as in Experiment 1 (Methods). Representative stimuli are shown. **(b)** Absolute threshold increases above baseline as a function of grating contrast (log scale) in the presence and absence of distracters in each visual field quadrant. Baseline thresholds were obtained from an independent series of up to 24 measurements in each quadrant, using high contrast (50% to 87%) gratings. High contrasts were used to allow comparison of the effects of variying both distracter and grating contrast against baseline thresholds representing the monkey's best possible discrimination performance without distracters. Average baseline thresholds in normal, V4, TEO and V4+TEO quadrants were, respectively, 6.37, 11.53, 10.15, and 11.75° in M1 and 5.93, 9.33, 21.61, and 29.50° in M2. Baseline thresholds in the lesion quadrants were significantly elevated compared to the baseline in the normal quadrant ($p < 0.001$) in both monkeys. The close-to-zero threshold increases for gratings of 50% and 87% without distracters replicate baseline thresholds obtained under the same conditions in experiment 1. Data were pooled over monkeys (eight thresholds per data point, on average). Error bars indicate s.e.; the absence of an error bar indicates s.e. smaller than the symbol size. Symbols above upper dotted lines indicate conditions in which no threshold could be determined in at least half of the measurements.

Discussion

In the absence of distracters, V4 and TEO lesions caused deficits in grating orientation discrimination which was most pronounced in the quadrant affected by combined V4 and TEO lesions. However, in agreement with previous studies[18–20,24], both monkeys still discriminated fine orientation differences in all lesion-affected quadrants. By contrast, distracters greatly increased thresholds in all lesion-affected quadrants, especially in the combined lesion-affected quadrant, but not in the normal quadrant. Deficit severity depended on the relative contrasts: the deficit increased when distracter contrast was increased, and decreased when the distracter contrast was decreased relative to target contrast. Distracter-induced deficits in the lesion quadrants were not attributed to either acuity deficits or failure to detect the target.

In agreement with these findings, two previous studies[16,17] reported impairment in detecting a target less salient (dimmer or smaller) than surrounding elements in monkeys with V4 lesions. However, in contrast to the stable deficits found in the present study, these deficits disappeared within a few hundred trials and reappeared transiently only when a new stimulus display was introduced. Differences in the behavioral task may help to explain this discrepancy. In the previous studies, monkeys saccaded to the target, defined as the 'odd man out' in an array of stimuli, without judging the target's features after its selection. Although target identification required some discrimination of target from distracters, the monkey needed to know only that it was different from the others, but not its specific features. By contrast, the monkeys in our study were required to discriminate a feature of the selected target at threshold level in the presence of distracters; the lesions specifically and permanently impaired this ability. Consistent with this interpretation, we found that the mere detection of a target grating among distracters—a task requiring minimal fine discrimination of any of the stimuli in the display—was unaffected by the lesions. In sum, although earlier studies suggest that area V4 may contribute to target selection even when this does not involve a fine analysis of the stimuli in the display, we demonstrate that V4 and TEO become crucial for fine discrimination of the target in the presence of distracters.

The inability of the animals to ignore strong distracters in the lesion quadrants is consistent with the view that, in V4 and TEO of the intact animal, top-down attention can bias a bottom-up competition among multiple stimuli in favor of the target at the expense of distracters[36,39]. The resulting competitive advantage of the target against distracters permits an accurate perceptual analysis of the target. V4 and TEO lesions eliminate the influence of top-down bias such that the outcome of the competition in the remaining, intact visual areas is determined solely by the relative physical strengths of target and distracters. As a result, grating orientation thresholds in the lesion-affected quadrants depended on distracter contrast. Indeed, one could interpret attentional effects in normal vision as equivalent to boosts in target contrast that allow it to win competition over distracters.

Physiological studies[33,34,36] show that competition and the effects of attentional bias on that competition are maximized for stimuli within a cell's RF. Thus, increasing RF size from lower to higher areas in the ventral stream hierarchy[1] should be accompanied by expanding spatial extent of this biased competition between stimuli. Smaller RFs in V4 than in TEO predict smaller regions over which distracting stimuli will influence target discrimination following V4 lesions than TEO lesions, just as we found. A study of biased competition using fMRI in human subjects yielded similar findings[45]. Furthermore, when target–distracter spacing was made too large for V4 and TEO cells to contribute to biased competition, lesions in V4 and TEO did not influence orientation thresholds measured with the grating. These results suggest that the contribution of a particu-

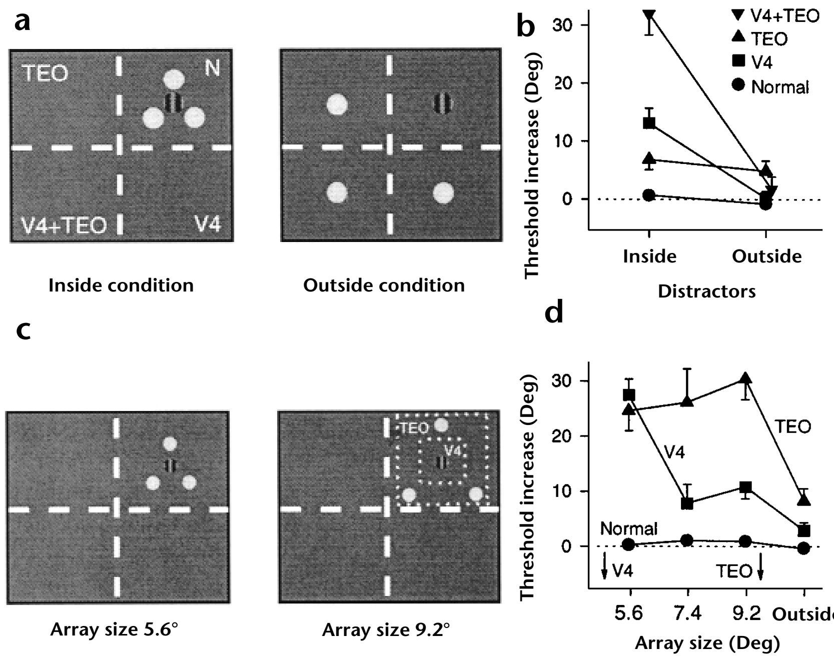


Fig. 4. Effects of spacing between target grating and distracters (both 50% contrast). **(a)** Stimulus arrays when distracters were inside the quadrant with the target (inside condition), or with distracters outside (outside condition). Stimulus parameters are as described in experiment 1 (Methods). **(b)** Threshold increases in inside and outside conditions (pooled over monkeys) compared against the same baseline as used in Fig. 3b. Each data point was based on 15 thresholds, on average (pooled over monkeys). Error bars are s.e. **(c)** Representative stimulus arrays made of a small grating and distracters (both 1.1° diameter, see Methods). Array size refers to the side of the square area containing all stimuli. Dotted lines indicate typical RF sizes in V4 and TEO at an eccentricity of 5.8°[43,44]. Drawings in **(a)** and **(c)** are approximately to scale, and represent the central 20° × 18° (width by height) of the stimulus monitor. Spacing between stimulus centers in the 5.6° stimulus array was identical to that in the inside condition in **(a)**, and to that in the arrays shown in Figs. 2a and 3a. **(d)** Threshold increases in M2 compared to baseline thresholds obtained without distracters in normal, V4 and TEO quadrants. Threshold increases are plotted as a functions of increasing spacing or array size. Arrows indicate typical RF sizes in V4 and TEO at the tested eccentricity[43,44]. Average baseline thresholds, based on eight threshold measurements in normal, V4 and TEO quadrants were 7.32, 16.53 and 25.32°, respectively. Each data point includes 12 thresholds, on average. Error bars indicate s.e. In the V4+TEO quadrant, no thresholds could be obtained when the distracters were within the same quadrant as the grating (not shown).

lar area to biased competition has a spatial extent limited by RF size, and that the monkeys' ability to distinguish targets from distant distracters dispersed over all quadrants was mediated by neurons in TE, whose RFs encompass all stimuli[1,7,31]. On the other hand, attentional mechanisms in intact area TE apparently did not have the spatial resolution necessary to separate targets from nearby distracters following lesions of V4 or TEO, despite the large RF size in TE.

How can we explain the relative sparing of simple orientation discrimination without distracters in the face of large impairments in attentional selection following V4 and TEO lesions? Remaining indirect corticocortical or corticosubcortical anatomical connections may convey orientation information processed in V2 to area TE. However, this pathway would lack critical stages of high-resolution attentional processing normally contributed by V4 and TEO.

Several influential theories of attention have been proposed to explain behavioral performance in search tasks, including texton theory[46], feature integration theory[47] and guided search theory[48]; in each, a target can either be selected in a parallel, quasi-automatic way or through a directed serial search, depending upon the physical properties of the target and surrounding distracters. According to a biased competition account of attention[36,39], the target wins a simultaneous competition with surrounding distracters, suggesting a more parallel than serial process. The debate about the parallel or serial nature of attention remains unsettled, as neither the single cell data nor the present lesion study allows a conclusive answer. Furthermore, both the mechanism by which biasing signals influence bottom-up competition between stimuli and the source of that signal remain unknown. However, only the biased competition model predicts the present results, including the critical role of relative contrast following the lesions and the differential effects of lesions on different-sized arrays. Testing the model in a variety of search tasks while measuring behavioral and physiological correlates of search performance may help to resolve many unanswered questions.

Methods

Two monkeys (M1, id#86042, and M2, id#RDG2) were used. Implant and lesion surgeries as well as behavioral testing followed NIH guidelines (protocol LN477, approved by NIH IACUC). Implant surgeries involved the placement of a post to immobilize the head and the introduction of an eye-coil in the sclera to monitor eye movements[49]. Comparable lesions were made in the two monkeys by aspiration of the gray matter.

To make the retinotopic 'mosaic' lesions in V4 and TEO, we exploited the separation of lower from upper field representations of V4, on the prelunate and inferior occipital convexities, respectively[43]. Thus, to restrict the lesion to the lower right quadrant of the visual field in V4, the cortex on the prelunate gyrus and adjacent cortex was removed in the left hemisphere (dorsal V4 lesion[20]). In the right hemisphere, a lesion of dorsal V4 was extended forward to the posterior temporal region to include the entire TEO representation in that hemisphere, based on sulcal landmarks[44]. This resulted in a lower left quadrant of the visual field affected by both the V4 and TEO lesion, as well as an upper left quadrant of the visual field affected only by the TEO lesion (**Fig. 1b**). Lesion reconstruction was based on coronal slices obtained with MRI (GE 1.5T, 1 mm thick, 256 × 160 or 256 × 192 matrix, 4NEX, FOV 10–11 cm). Figure 1a suggests some encroachment of the TEO lesion in monkey M2 into area TE. If this encroachment had been significant, then discrimination performance in the 'normal' quadrant of monkey M2 would have been adversely affected, since RFs in TE extend into the ipsilateral hemifield. However, grating orientation thresholds without distracters in the normal quadrant did not differ ($F_{1,59} = 1.983$, $p = 0.164$) from thresholds obtained with similar grating stimuli in the normal quadrant of two other monkeys with a lesion confined to dorsal V4 (ref. 20). The same finding held for monkey M1 ($F_{1,59} = 0.652$, $p = 0.423$).

Stimuli used in experiments 1–3 were phase-randomized gratings of low spatial frequency, presented in a circular aperture. Gratings were presented at an eccentricity of 5.8°; trials were aborted for eye movements outside a 1.5° square window centered on the fixation point. The edges in the grating stimulus consisted of a 0.1°-wide random noise band (50% pixels randomly turned on or off), which masked artifacts associated with the presentation of orientations close to principal axes on a digitized screen. In all experiments except experiments 3 (**Fig. 4d**) and 4 (the acuity test), grating spatial frequency was 1.1 cpd in M1 and 0.6 cpd in M2. During the acuity test, only vertical gratings with intact rather than noisy edges were presented within a circular aperture of 2.2° in M1 and 4.4° in M2. Spatial frequency was 2 cpd and grating diameter was 1.1° in the last part of experiment 3 (M2 only, **Fig. 4c**). Distracters darker or brighter than the background and of the same diameter as the grating were shown in triplets, chosen randomly in each trial from eight predefined distracter configurations. Grating position remained fixed. Distracters were positioned close to the grating except in experiment 3, for which distance between target and distracters varied. To calculate grating contrast, a Michelson index obtained by subtracting dark stripe luminance from white stripe luminance was expressed as a percentage of the sum of the two luminances. Similarly, distracter luminance was subtracted from the background luminance and the result expressed as a percentage of the sum of those two luminances to calculate distracter contrast. Background luminance and the average grating luminance were equal and in the mesopic range.

Orientation thresholds were determined by dividing orientation difference by 1.25 after four consecutive correct responses and multiplying by 1.25 after a single incorrect one. Using this method, orientation differences converge around a level corresponding to an 84% correct performance[50]. The measurement ended after a maximum of 120 trials or after 14 reversal points. The 84% correct threshold was calculated as the geometric mean of all reversal points[50] except the first 4, such that each threshold was based on approximately 100 trials.

A typical testing session consisted of four consecutive threshold measurements in each quadrant, with the order between quadrants randomized over sessions. During a single session, one experimental condition was tested (one distracter contrast, one grating contrast or one distance between grating and distracter). Both monkeys typically executed up to three testing sessions daily, and the experimental condition in each session was picked randomly, except in experiment 2. In that experiment, data in the three distracter conditions (0%, 10% or 50%) were obtained in three separate blocks of sessions during which grating contrast was decreased from session to session. The order of the three blocks of distracter conditions was chosen randomly. The data were log-transformed to homogenize variance, and analyzed using ANOVA and *post-hoc t*-tests. Thresholds obtained preoperatively showed no asymmetries between quadrants. Postoperative experiments were preceded by training to achieve stable thresholds.

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